Mastodons from the Miocene of Saudi Arabia

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Synopsis

Mastodon dental remains from Ad Dabtiyah, Saudi Arabia, are assigned to *Gomphotherium cooperi*, a species hitherto known only from the basal Miocene of Dera Bugti, Pakistan. The Ad Dabtiyah population would best fit a late Lower Miocene or earliest Middle Miocene date—equivalent to the middle Orleanian of Europe and coming between Rusinga and Maboko in east Africa. A right $M^2 + M^3$ from 60 km south of Ad Dabtiyah is tentatively included in *G. cooperi*.

Introduction

All but one (M.42946) of the Proboscidea described in this paper come from Ad Dabtiyah, Saudi Arabia, and were collected by P. J. Whybrow, H. A. McClure and the late W. R. Hamilton in 1974. The locality is situated at 26° 27′ 02″ N, 48° 35′ 24″ E (Hamilton *et al.* 1978; see also Whybrow *et al.*, this issue, p. 375) where the fossils occur in continental deposits thought to be laterally equivalent to the nearby extreme limits of the marine Miocene Dam Formation.

Register numbers of specimens refer to the collection of the British Museum (Natural History), London. Measurements (Table 2) are given in millimetres.

In mastodons the pretrite is the lingual half of an upper molar loph and the labial half of a lower molar lophid. The posttrite is the remaining half of each loph or lophid. Pretrites become worn in advance of the corresponding posttrites.

Systematics

Order **PROBOSCIDEA** Illiger, 1811

Family **GOMPHOTHERIIDAE** Hay, 1922

Genus ***GOMPHOTHERIUM*** Burmeister, 1837

Gomphotherium cooperi (Osborn, 1932)
Figs 16–22

1932 *Trilophodon cooperi* Osborn: 3; figs 1–2.

MATERIAL. Measurements are given in Table 2.

M.42940 Conjoined left M_3 and back of M_2. The rear lophid of M_3 has begun to wear. Figs 16, 22.

M.42941 Left lower tusk. Fig. 17.

M.42942 Much of right mandible with M_3. M_2, present in life, is now missing. All lophids of M_3 are in wear. Only the back of the rostrum is present. Fig. 18.

M.42943 Right M^3. The front loph has begun wear. Figs 19, 22.

M.42944 Back of left M_3. Lophids not yet in wear.

M.42945 Left M_3. Wear has barely started on the second lophid; incomplete posteriorly. Figs 20, 22.

M.42946 Conjoined right M^3 and M^2. M^2 is heavily worn and the front two lophs of M^3 are worn. Rear of M^3 is damaged and incomplete. Figs 21–22. The locality for this specimen is about 10 km west of Jabal Uray'irah, an area about 60 km south of Ad Dabtiyah, where undifferentiated deposits are thought to include equivalents of the Dam and Hofuf Formations (Steineke *et al.* 1958). The specimen was collected 40–50 years ago by oil company geologists. It is questionably included in *G. cooperi*.

M.42947 Lateral part of proximal left ulna from Ad Dabtiyah. It can be assumed to be conspecific with the teeth M.42940–5.

M.42948 Partial right scapula from Ad Dabtiyah. Again conspecificity with the teeth can be assumed.

Fig. 16 *Gomphotherium cooperi.* Occlusal view of left M_3 and back of M_2, M.42940, from Ad Dabtiyah. Anterior side to the left. × 0·75.

DESCRIPTION. The teeth all come from one or more species of bunodont, trilophodont mastodon. Except for M.42942 they are preserved only as crowns which has made identification as uppers or lowers less secure in some cases.

The M_3s have four lophids plus a posterior cingulum; the M^3 M.42943 has three lophs and that of M.42946 has four. The third and fourth lophs and lophids show signs of chevroning (forwardly-directed indenting in their centres). The cones and conules of the lophs and lophids are moderate- to high-crowned. In M.42940 and M.42943 they give the appearance of growing out of a basal shelf and the lower parts of their sides are not closely pressed to one another. Small cingular tubercles may be visible between cones. Besides the main (outside) cone in each half loph or lophid there is one additional conelet budded off towards the longitudinal median line of the tooth. M.42943 shows an irregularly surfaced swelling on the rear of the posttrite of the anterior loph, which could be taken as a rudimentary posterior conelet.

The lower tusk M.42941 is peg-like, has a slight twist, a concave upper surface and convex lower surface in cross section, and longitudinal grooves and striations on its lower surface. The latter feature is reminiscent of hippopotamus canines. No enamel band is visible along its outer surfaces. The length, as preserved, is 345 mm and its mid-length diameters 45·3 × 28 mm.

The two postcranial bones, M.42947-8, will not be considered further.

Table 2 Measurements in mm of molars of *Gomphotherium cooperi* (Osborn) from Saudi Arabia.

Specimen		Maximum length	Width across 1st loph(-id)	Maximum width
M_3	M.42940	136	*c.* 60·0	64·2
M_3	M.42942	147	64·3	70·6
M_3	M.42945	*c.* 157	*c.* 69·0	*c.* 76·1
M^3	M.42943	148	*c.* 63·0	66·8
M^3	M.42946	*c.* 147	76·1	*c.* 78·0
M^2	M.42946	*c.* 108	—	67·0

Fig. 17 *Gomphotherium cooperi.* Above: dorsal view of left lower tusk, M.42941, from Ad Dabtiyah. Below: lateral view of same tusk. Inset: transverse section across middle of tusk, medial side to the left, dorsal to the top. × 0·5.

Background to comparisons

Work by Tobien and Tassy since 1970 has greatly improved our grasp of mastodon evolution. Even if not found to be correct in all details their various proposals do at least add up to a comprehensible framework (see Tassy 1983*a*, *b* and references; Tobien 1973). It seems that the following groups of Neogene (effectively post-Egyptian Fayum) Old World mastodons can be recognized.

1. Zygodont or ridge-toothed mastodons of Family Mammutidae, *Eozygodon* Tassy & Pickford (1983) in Africa and *Zygolophodon* Vacek in Eurasia, the latter surviving until the later Pliocene. The remaining mastodons mentioned below are all bunodont.
2. *Gomphotherium*, an early trilophodont mastodon of Family Gomphotheriidae. The European type species, *G. angustidens* (Cuvier), has been known since Cuvier's time and *G. cooperi* and *G. browni* (Osborn) come from the basal Miocene Nari Formation (its upper part) at Dera Bugti, and from the Middle Miocene Chinji Formation, respectively, of Pakistan. Raza & Meyer (1984: 45) place Bugti in the Chitarwata Formation.
3. Shovel-tusked trilophodont mastodons belonging to *Platybelodon* Borissiak, *Protanancus* Arambourg and *Archaeobelodon* Tassy 1983*b*, best known from Asia and Africa. This group is put in the subfamily Amebelodontinae of the Gomphotheriidae, named after the North American type genus.
4. The persistently trilophodont *Choerolophodon* Schlesinger, which develops a crowded and irregular pattern of cones and conules on its molars. This genus also is accorded subfamily rank within the Gomphotheriidae.
5. The tetralophodont mastodons *Tetralophodon* Falconer & Cautley, mainly from the *Hipparion* faunas of Europe, and *Paratetralophodon* Tassy 1983*a* from the Dhok Pathan Formation of the Siwaliks. They are put into subfamily Gomphotheriinae.
6. More advanced relatives of *Tetralophodon*, comprising *Stegolophodon* Schlesinger and *Stegotetrabelodon* Petrocchi which could in their turn be close to *Stegodon* Falconer, *Primelephas* Maglio and later elephants. The differences in molar teeth of these four genera, present though they are, are outweighed by the similarities. Their family affiliation has long been variably interpreted.

The Arabian mastodon remains are clearly trilophodont and bunodont and the central questions are whether they belong to *Gomphotherium* or the Amebelodontinae and how far these groups can be separated anyway.

Until recently *Gomphotherium angustidens* was thought to have lived in Europe from the middle of the Orleanian (late Lower Miocene) as at Artenay, France, until the Vallesian (early Upper Miocene). The name of *G. angustidens* has been used as a blanket and convenient designation for any trilophodont, bunodont mastodon and Osborn (1936: 340; fig. 299) selected as lectotype an M_2 from Simorre, a middle or late Astaracian locality. However Tobien (1973: 255) drew attention to finds of shovel-like mastodon tusks in western Europe and Tassy (1983*b*: 462) founded the genus *Archaeobelodon* for them. Tassy has also emphasized that at Sansan, France (early Astaracian) and in Africa and southern Asia the most abundant early mastodons appear to be amebelodontines.

Gomphotherium is held to have strong upper tusks of oval or triangular cross section, twisting outwards and downwards, and with a broad enamel band along the lateral to ventral surface. The lower tusks are short with a rounded oval cross section (Tobien 1973: fig. 3 nos 1–3) and concave dorsal surface. They are set in a long rostrum and Tobien refers to them as peg-tusks. Amebelodont lower tusks are more flattened and can reach enormous dimensions, as in the Asiatic *Platybelodon* (see Osborn 1936: figs 426, 437). Internally they may acquire a medulla of close-packed dentine tubercles instead of laminated dentine (Tassy 1983*a*: pl. 1, fig. 2; Gaziry 1976: pl. 3, fig. 2). Much taxonomic weight has been put on these tubercles, which are presumably a mechanical response to either pronounced flattening or increased size (as in Schlesinger 1917: pl. 34, fig. 2) of lower tusks. However they are not yet present in early amebelodonts (Tassy 1983*a*: 126–127) so cannot help to define the subfamily. Upper tusks of amebelodonts

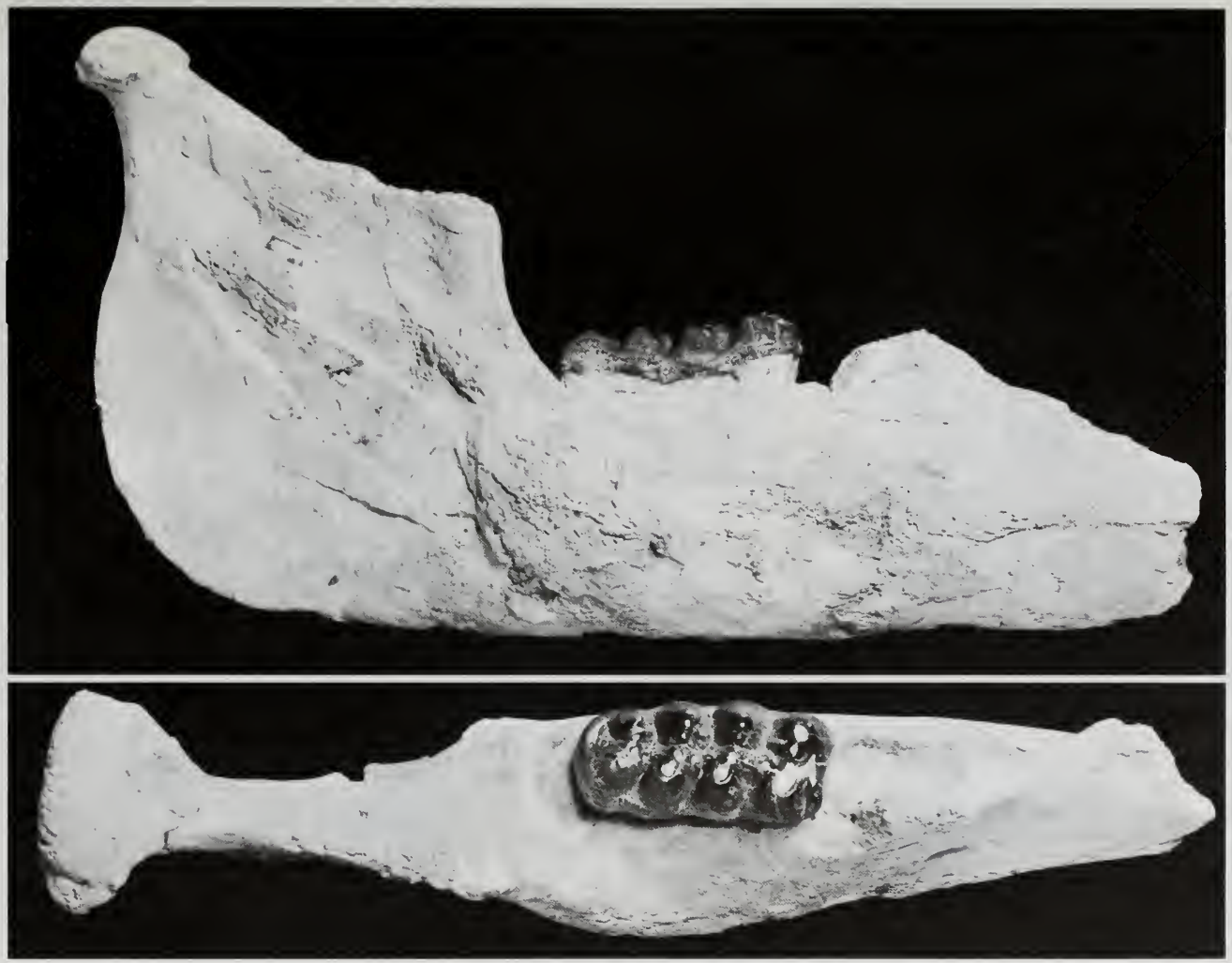

Fig. 18 *Gomphotherium cooperi.* Lateral and dorsal views of right mandible with M_3, M.42942, from Ad Dabtiyah. × 0·25.

Fig. 19 *Gomphotherium cooperi.* Occlusal view of right M^3, M.42943, from Ad Dabtiyah. Anterior side of the right. × 0·75.

are alleged to be small; this is obviously true in relation to their own lower tusks, but less so in relation to *Gomphotherium* upper tusks (Osborn 1936; compare figs 416 A2 and 436). Another feature of amebelodonts is the narrowness of their molars and Tobien (1973: fig. 9) demonstrates this as between Asiatic *Platybelodon* and European and North American *Gomphotherium*. Also considered helpful is the development of posterior conules on the posttrites which may give rise to a more fully trefoil pattern as on the pretrites.

Tassy (1979: 267; 1983*b*: 466) referred *Protanancus macinnesi* Arambourg of the lower Middle Miocene of Maboko, Kenya, to the Amebelodontinae. Its molars are certainly narrower than in European *Gomphotherium* and sometimes there is an indication of posterior conules on the posttrites (MacInnes 1942: pl. 4, fig. 2). Moreover somewhat widened lower tusks are known from Maboko. Tassy (1979: 267) took the mastodon of the Lower Miocene of

Fig. 20 *Gomphotherium cooperi.* Occlusal view of left M_3, M.42945, from Ad Dabtiyah. Anterior side to the left. × 0·75.

Fig. 21 *Gomphotherium cooperi*. Occlusal view of right M^2 and M^3, M.42946, from 60 km south of Ad Dabtiyah. Anterior side to the right. × 0·75.

Rusinga, Kenya, as also an amebelodontine; the flattened lower tusk from Loperot (Maglio 1969) may be another earlier record than Maboko, although Pickford (1981: 90) has some doubts. Tassy (1983*a*: 116) put into *Protanancus* the common mastodon of the Chinji Formation, *P. chinjiensis* (Pilgrim), which is somewhat advanced on *P. macinnesi* in, for example, the more obvious posterior conules of the posttrites (Tassy 1983*a*: fig. 10).

The narrow molars and high cones of *Protanancus* and *Platybelodon* are definitely different from *Gomphotherium*, either *G. angustidens* of Europe or the more rarely preserved *G. browni* (Osborn 1936: fig. 416) which is contemporaneous and sympatric with *Protanancus chinjiensis*. As regards posterior conules of the posttrites, these can sometimes be seen in *Gomphotherium*, as on the front lophid of M_3 of the *G. browni* holotype.

The relationships of *Gomphotherium cooperi* are problematical and it could be a junior synonym of *G. inopinatus* (Borissiak & Beliaeva) of Kazakhstan (see Osborn 1936: fig. 224). The holotype of *G. cooperi* is a mandible, M.12181 (Osborn 1936: fig. 222). Its M_3, and others from Bugti, have length/width proportions closer to the Maboko and Rusinga amebelodontines than to European *G. angustidens*. However, three Bugti M^3s, M.12185, M.12190 and the smaller M.12180 are as wide as in *Gomphotherium*. Tassy (1983*a*: 259) surprisingly assigned a Bugti M_3 to *Choerolophodon*. The tooth (cast M.11050) is longer than *Choerolophodon* M_3s from Maboko and his idea may be that some shortening of M_3 occurred in the earliest *Choerolophodon*.

In western Europe the distinction between the amebelodontine *Archaeobelodon* and *Gomphotherium* can be a matter of some difficulty, especially where isolated cheek teeth are involved (Tassy 1983*b*: 463). It is also noticeable that the amebelodont incisors recorded by Tobien (1973: fig. 15, nos 4–8) come from Sansan and La Grive, France, localities considerably postdating the arrival of Proboscidea in Europe. If the amebelodontine did evolve from earlier peg-tusked gomphotheres (Tobien 1973: fig. 3, nos 1–3), this would be out of line with Tassy's (1979: 265) view of the plesiomorphy of flattened incisors, but Tassy himself (1983*b*: 465) affirms that *Archaeobelodon* was present in Europe well before the time level of Sansan. The less extreme widening of the tusks of *Archaeobelodon* than in the Asian *Platybelodon* suggests the possibility of regional or continental variation in this character. The documentation of the all-important *Gomphotherium* remains from En Péjouan (Tassy 1983*b*: 463) is needed to establish that *G. angustidens* is indeed a species additional to and continentally sympatric with the western European amebelodontine.

The rest of this paper is mainly concerned with molar teeth, and those coming from Europe and used in comparisons will be referred to in the traditional manner as *Gomphotherium* or *G. angustidens*.

Comparisons

Against this background comparisons can be made between the Ad Dabtiyah mastodons and other relevant material.

M.42940. The M_3 is the only tooth worth considering in detail. It differs from M_3s of Sansan by being smaller, less robust, lower-crowned, and the lophids being more separated at their bases. This last character gives the appearance of the lophids having grown from a basal shelf and is reminiscent of *Zygolophodon*.

It is similar to the Rusinga M_3 M.15300 (MacInnes 1942: pl. 6, fig. 8) but lacks the irregular cingular tubercles evident in M.15300. It also seems to have less sign of swellings (? incipient conelets) around the lophids. It is not so narrow (Fig. 23, smallest reading for X) and is widest across the third instead of the second lophid. It is also very like the Bugti M_3s but shorter than M.12183, with less chevroning of the third lophid than in M.11050, and perhaps with smaller posterior conules of the pretrite trefoils, i.e. smaller conules between the lophids.

It has one less lophid than M_3s of Maboko *Protanancus macinnesi* and less or no chevroning of the fourth lophid. It has a better developed fourth lophid and less chevroning than Maboko *Choerolophodon* M.15542 (MacInnes 1942: pl. 6, fig. 7).

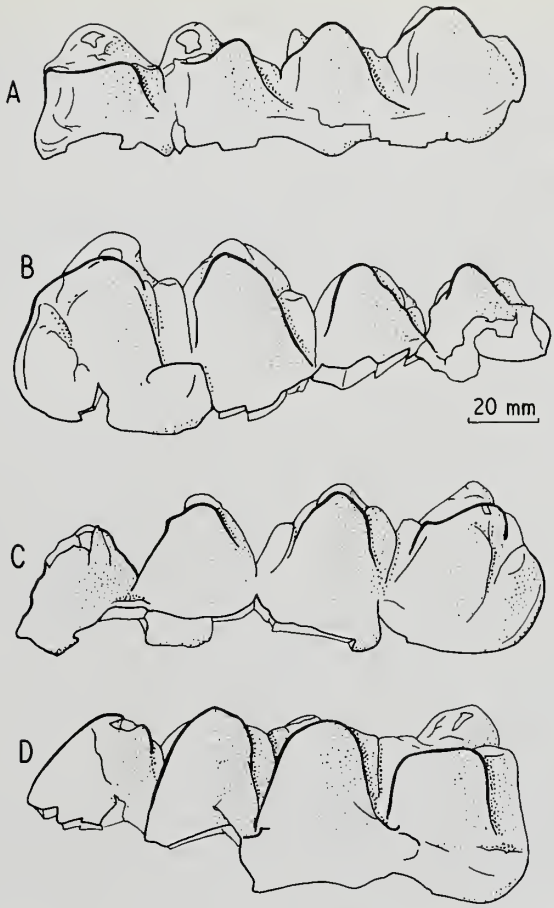

Fig. 22 *Gomphotherium cooperi.* Labial views of molars. A–C, from Ad Dabtiyah. A, left M_3, M.42940. B, left M_3, M.42945. C, right M^3, M.42943. D, right M^3 from 60 km south of Ad Dabtiyah, M.42946.

It looks very like the Artenay M_3 of Ginsburg & Antunes (1966: pl. 3, fig. 2) but is possibly lower-crowned. At first sight it also looks narrower but this is not borne out by Ginsburg & Antunes' measurements of length × breadth (179 × 82 mm) nor by my own measurements from their picture.

M.42941. The dorsal concavity of the tusk is very evident but the width is not sufficient for it to fit an amebelodontine (Tobien 1973: fig. 15).

M.42942. The M_3 in the mandible is better preserved and slightly more worn than the very similar M.42940. Its lophids look less as if they are growing out of a shelf. It is more evenly wide along its length instead of having the third lophid noticeably the widest. The posterior lobes of the pretrite trefoils, consituting the conules which lie centrally between the lophids, are small as in M.42940 and no larger than in Rusinga M.15300. These conules appear to be smaller than in M_3s from Bugti. The third lophid is less chevroned than in Bugti M.11050.

Its length/breadth proportion looks similar to the Artenay M_3 of *G. angustidens* (see Ginsburg & Antunes 1966: pl. 3, fig. 2), but the latter looks as if it has less marked anterior conules of the pretrite trefoils and a more obvious shelf from which grow the lophids.

M.42943. This M^3 differs from Sansan examples, e.g. 32534, by being smaller, narrower, lower-crowned, with three instead of four lophs and with less of an anteromedial cingulum. It also has only one, not two, conelets budded off towards the median line on each posttrite loph.

It is higher-crowned than the Rusinga M^3 M.15318 (MacInnes 1942: pl. 5, fig. 3) and has less of a cingular shelf and no obvious tubercles decorating the shelf labially and lingually.

It is narrower than the Bugti M^3s M.12185 and M.12190, and shows stronger development of the posterior lobes of the pretrite trefoils on lophs 2 and 3.

It differs from the Maboko *Protanancus* by having three instead of four lophs somewhat more widely spaced, being lower-crowned and showing less exaggerated anterior lobes on the pretrite trefoils of lophs 2 and 3.

M.42944. Little can be noted about this back of a left M_3.

M.42945. This M_3 looks more advanced than M.42940 in that it is larger and higher-crowned.

It differs from Sansan M_3s by being slightly lower-crowned and less robust and having more trace of a basal shelf between the front and second lophid row.

Its fourth lophid is less developed than in most of the M_3s illustrated by Bergounioux *et al.* (1953) from the Lisbon 'middle Helvetian Vb' faunas, thought to be of late Orleanian age. It is also lower-crowned than some of these M_3s. It would fit better with the small number of M_3s illustrated from the earlier 'upper Burdigalian IVb' faunas of middle Orleanian age (Bergounioux *et al.* 1953: figs 125, 143, 147, 148, 266). The IVb fauna, later called the R2 fauna, is stratigraphically positioned between the start of N7 and somewhere within N8 of the Blow marine planktonic foraminiferan scale (Van Couvering & Berggren 1977: 299). All the non-zygodont Portuguese mastodons were accepted as *G. angustidens* by Tobien (1973: 207).

It is higher-crowned and wider than Rusinga M.15300.

It is difficult to judge whether, when complete behind the fourth lophid, it would have been as long as the Maboko *Protanancus*, i.e. longer than in Rusinga M.15300. The third lophid may be less chevroned than in Maboko or Chinji *Protanancus*.

The front two lophs of M.42945 are very similar to the same part of the M_3 of *Gomphotherium browni* (AMNH 19417, BM(NH) cast M.15035). Possibly the posterior lobe of the posttrite of the first lophid is less marked than in *G. browni*. The tooth is longer and more robust than in *G. cooperi* M.12181, but has about the same crown height.

M.42946. The M^3 is as long as M.42943 and wider as well. There appear to have been four lophs and the second posttrite had a posterior conule. There were probably two conelets budded off medianwards on each posttrite loph, although preservation and wear impose some uncertainty about this.

At the back of the M^2 the talon has been incorporated into the third pretrite wear facet. The size of the talon in earlier wear would have been about as in the M^2 on the Bugti palates M.12178–9, the normal *Gomphotherium* size.

Its relatively great width is like the Artenay M^3 of Ginsburg & Antunes (1966: pl. 4, figs 2, 3), but its fourth loph is more advanced. It is very like the Sansan M^3 32534, except for the absence of a medianmost lobe on the first pretrite trefoil of the latter which may be fortuitous.

Compared with Maboko *Protanancus macinnesi*, the M^3 on M.42946 is wider but otherwise very similar. Possibly the wings of the pretrite trefoils are better developed in *P. macinnesi*.

It is similar to the M^3 of *G. browni* (cast M.15035; Osborn 1936: fig. 416) but the chevron effect on the third loph may be more pronounced and the lobes of the pretrite trefoils have less of an appearance of being gathered into the line of the lophs. A median longitudinal groove, incipient on M.15035, is not apparent on M.42946.

Compared with the Bugti M^3s M.12185 and M.12190 it is more advanced in its fourth lobe and higher cones. Again the posterior lobe of the pretrite trefoil on the first loph of M.42946 is better developed than in the Bugti teeth. The Bugti teeth could be foreshadowing the condition of *G. browni*.

Coming from a different locality and with a definitely advanced morphology, M.42946 may be a different species from the other Arabian mastodon teeth but for the present it need not be separated from them.

Conclusions

There is evidently a range of variation among the Arabian mastodon teeth. M.42940 is small like Rusinga and Bugti M_3s but less narrow than in the single Rusinga example. M.42945 is larger and higher-crowned. All three Ad Dabtiyah M_3s are wider than in the Maboko *Protanancus* and could most probably belong to a *Gomphotherium*, an attribution compatible with the peg-like lower tusk, M.42941.

The M^3 M.42943, however, is narrower than in the Sansan, Artenay or Bugti gomphotheres, and hence appears more akin to an amebelodont.

On balance it seems best not to split these teeth into different species but to take them all as one species of *Gomphotherium*. *G. browni* is poorly known and it differs in that its molars appear too large and advanced and the lower incisors have a more rounded cross section

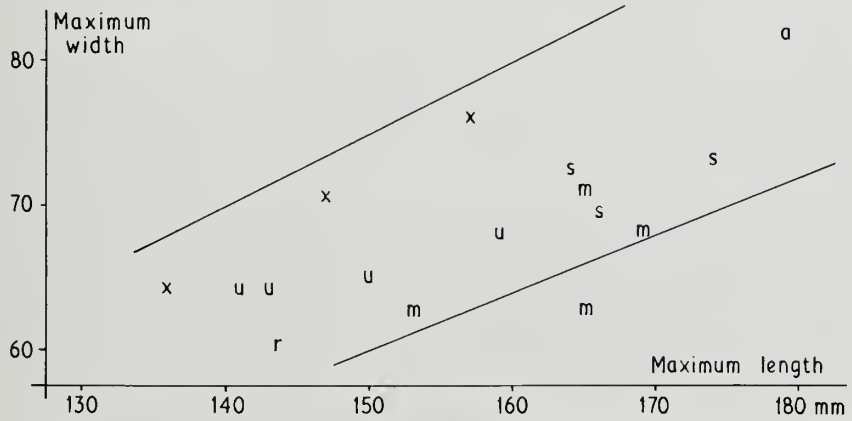

Fig. 23 Width/length proportion for some mastodon M_3s. X = Ad Dabtiyah *Gomphotherium cooperi*; a = Artenay *G. angustidens*; m = Maboko *Protanancus macinnesi*; r = Rusinga amebelodontine; s = Sansan *G. angustidens*; u = Dera Bugti *G. cooperi*. Upper diagonal line is that along which width is 50% of length; the lower line is 40%.

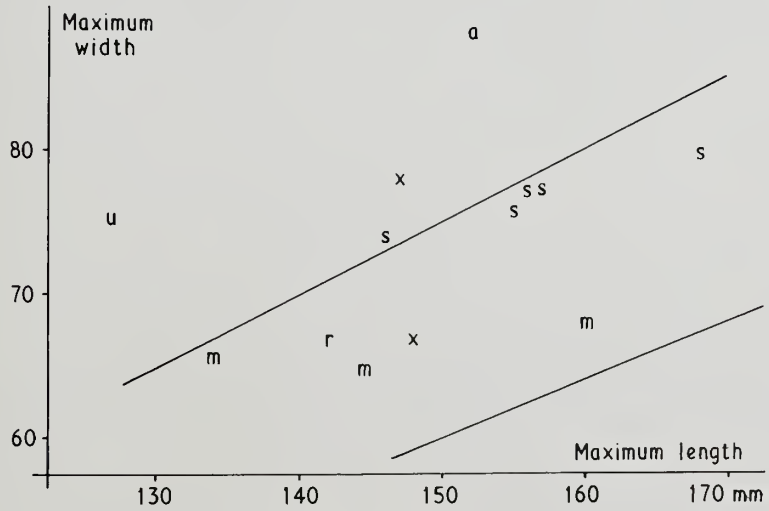

Fig. 24 Width/length proportion for some mastodon M^3s. Symbols and diagonal lines as in Fig. 23.

(Tassy 1983*a*: fig. 25A). *G. angustidens*, at least as represented in Sansan and later localities, is also more advanced. Probably the best designation for the Arabian species is *G. cooperi*. Bugti specimens included in this species show a wide range of variation between narrow M_3s and wide M^3s, but the unerupted M_3 of the holotype mandible M.12181 could not be improved upon as a match for a species embracing M.42940 and M.42945.

Size alone is not a good guide for correlation since European *G. angustidens* has a considerably greater size range than shown on Figs 23–24 for the small BM(NH) sample from Sansan. It would not be reliable to take the small size of the Arabian teeth on these graphs as indicating a pre-Astaracian time of occurrence. Nor is the appearance that the lophs or lophids are growing up from a basal shelf or plate a satisfactory character to use for correlations. Such a shelf is seen in M.42940 and some other early mastodon teeth, but it may also be found in later mastodons, e.g. M.7228, a cast M_3 of '*Mastodon pyrenaicus*' Lartet identified by Tassy (1977: 1391) as an Astaracian occurrence of *Tetralophodon longirostris* (Kaup). Hence the similar structure of M.42940 cannot be regarded as a primitive character indicating an early time level.

We are left with the number and height of lophids and lophs, and these suggest that the Ad Dabtiyah specimens lived at a period before the Maboko level in Africa or Sansan in Europe. They are probably not as old as Rusinga in east Africa, and in the European sequence they would best fit a middle Orleanian time level. They are probably younger than the Dera Bugti *G. cooperi*.

M.42946, from 60 km south of Ad Dabtiyah, looks like a *Gomphotherium* as advanced as that at Sansan and could come from a higher stratigraphical level than at Ad Dabtiyah. It does not appear to be evolving towards *G. browni*.

The Arabian mastodon teeth have not improved understanding of the relations between *Gomphotherium* and amebelodontines, although the dorsal concavity of the tusk M.42941 supports the idea that they were closely linked.

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